The Development of the Calcareous Parts of the Lantern of Aristotle in Echinus Miliaris.

By D. W. Devanesen, M.A.

(Communicated by Prof. E. W. MacBride, F.R.S. Received April 12, 1922.)

[Plates 11–15.]

CONTENTS.

		PAGE
1.	Introduction	468
2.	Method	469
3.	The Jaws	470
4.	The Epiphyses	470
5.	The Rotulæ	471
6.	The Compasses	471
7.	The Teeth	472
8.	Discussion	478
9.	A comparison between Giesbrecht's account of the development of the urchin-tooth as revealed by its root-end in the adult and the construction of the same as seen in the young urchin	481
10.	Summary	483
11.	References	483
12.	Explanation of Plates	485

1. *Introduction.*

This investigation was suggested to me by Prof. E. W. MacBride, F.R.S., to whom my thanks are also due for kindly placing at my disposal two metamorphosing plutei and a considerable number of young imagos of *Echinus miliaris,* all of them fixed in absolute alcohol.

In the year 1892, Lovén (3) made a few observations on the embryonic elements of the calcareous lantern in *Goniocidaris canaliculata,* a Cidarid with a direct development. He also examined the same structures in two young urchins which, as he himself admits, were of doubtful identity and in a state of bad preservation. In the same year, Théel (7), who was working at the early development of the cake-urchin, *Echinocyamus pusillus,* described certain early stages of the lantern in the young urchins. After these researches of Lovén and Théel, it appears that no attempts have been made to study the development of the lantern ossicles in greater detail and with closer scrutiny.

It must be stated, however, that in the year 1903, in a near relative of *Echinus miliaris,* viz., *Echinus esculentus,* though the origin and homology of the lantern-cœlom had been investigated by Prof. MacBride (4), the calcareous structures it contains remained untouched. One of the obstacles to their study was the fact that non-decalcified specimens could not be sectioned satisfactorily by ordinary methods; and even if they could be sectioned, there was the enormous difficulty of reconstructing, either mentally or otherwise, a very complicated system of ossicles. But, happily, these difficulties were obviated by following a unique idea very kindly suggested to me by Prof. MacBride. He thought that if one could cut away just the top part of the shell, then, after some slight maceration, one could see the lantern ossicles below. By employing this method were obtained several important facts which are recorded in this paper. I here take the opportunity of expressing my deep indebtedness to Prof. MacBride for the many valuable suggestions made and for the frequent advice given throughout the course of this investigation, and for kindly reading the manuscript.

2. *Method.*

The process of double imbedding in celloidin* and paraffin was employed, and the "Jung" sliding microtome was used for sectioning. The latter instrument exactly suited my purpose, viz., making an opening at the aboral surface of the young urchin. Any slight error in orientation can readily be corrected in the course of sectioning by the side-to-side and front-to-rear adjustments of the object-holder. I must remark, however, that it required some skill and judgment to cut away just enough of the aboral part of the shell so as not to damage the lantern below.

When enough of the shell had been sectioned off, the paraffin was dissolved out in xylol, and the celloidin was removed by using a mixture of equal parts of ether and absolute alcohol. The young urchin was then passed through decreasing strengths of alcohol and finally brought into distilled water when it was ready to be treated with "Eau-de-la-barraque." In this liquid was discovered an ideal macerating solution for the young urchin material. While it does not act so vigorously as caustic-potash, for instance, it dissolves in a given time just enough of the tissues to enable one to see through them the contained transparent ossicles. This maceration was watched under a low power of the microscope and it lasted never more than a few seconds. The young urchin was quickly transferred to distilled water and passed through increasing strengths of alcohol, then into xylol, and finally mounted in xylol-balsam in the cavity of an excavated slide. Such whole mounts, when illuminated with a "Nernst" electric lamp and examined with a 2 mm. oil immersion lens, show the ossicles of the lantern very well indeed.

Entire embryonic teeth were obtained by applying gentle pressure, with a mounted-needle under microscopical guidance, to a well-macerated young urchin. The shell breaks away leaving the lantern in the centre. By further manipulations with the mounted-needle the teeth were separated, dried, and mounted in xylol-balsam. An examination of whole embryonic teeth revealed several facts which were hitherto unknown and which threw fresh light on their morphology.

---

* The imbedding in celloidin was done according to Gilson's rapid process (Lee's 'Vade Mecum,' 8th edition, p. 104).

3. *The Jaws.*

In describing the development of the lantern ossicles, it is perhaps well to begin with the jaw and proceed upwards. Each jaw, or a pair of "alveoli," is developed from a pair of tri-radiate spicules deposited in an inter-radius of the "echinus-rudiment" of the metamorphosing pluteus; two rays of each rudiment of an alveolus are found embracing a tooth, one on the inner side and the other on the outer side, while the third ray is seen to stretch aborally and towards the rudiment of an "epiphysis" in the contiguous radius (Plate 11, fig. 1; *R.A.*). The next step in the growth of these spicules consists in the branching of the three rays at their ends and in budding new off-shoots over their body; these subsequently join end-to-end. By repetitions of this process, there results a perforated ossicle having more or less the shape of an adult alveolus. In fact, the rudiments of the alveoli, like all other elements of the lantern, with the exception of the teeth, follow the usual method of ossicle growth among echinoderms; but, as compared with the growth of the epiphyses and the rotulæ, for instance, these grow mainly along their vertical axes. This fact enables one to account for the great height of the lantern in urchins generally. This vertical growth of the jaw has caused the ossicles above to be pushed farther and farther away from the oral region. In the very early stages, as may be expected, one finds all the rudiments of the lantern occupying a comparatively low position.

The upward and radially-directed growth of each alveolus results in a junction between it and the rudiment of an epiphysis in the adjoining radius. Each jaw, therefore, bears on the top two epiphyses belonging to different radii.

4. *The Epiphyses.*

One finds their earliest traces as pairs of triradiate spicules situated in each radius of the "echinus-rudiment," far below the rotulæ, and above the level of the jaw-rudiments. Each spicule grows by the usual method, and when a more or less rectangular plate is formed, each epiphysis gives off from its outer corner, in the proximity of a tooth, a process; the two processes belonging to a pair of epiphyses diverge from one another (Plate 14, fig. 5, *O.E.*). One outgrowth meets, over the "foramen magnum" and on the outer side of a tooth, another—I say "another" advisedly, for it is not its fellow—belonging to an epiphysis of a different but adjoining pair (Plate 15, fig. 6, *O.E.*). Both processes together form at this stage a comparatively flat bridge, the arch-form being attained later. It is significant that this bridge was not developed by the palæozoic Echinocystoida, Perischo-echinoida, Cidaroida, Holectypina, and two orders of Centrechinoida. According to Jackson (2, pp. 179 and 183) this is an important character found only in the four families of the Temnopleuridæ, Echinidæ, Strongylocentrotidæ, and Echinometridæ, comprising his new sub-order Camerodonta. Evidently the presence of this bridge for the attachment of the protractor muscles is a sign of advance belonging to a late period in the phylogeny of the sea-urchins.

The two epiphyses connected by their extensions are further in contact below with the same jaw, so that it is customary in text-books to designate them as a pair of epiphyses. But, as far as one could make out from the position of their rudiments, it strikes one that the two epiphyses which lie one on each side of and below a rotula form a pair. This being so, one may say each pair maintains its radial position in the adult, there being no diverging of the epiphyses from a radius. On the contrary, as has been mentioned already, the two alveoli of each jaw, growing aborally like the limbs of a V, each effect a junction with an epiphysis belonging to an adjacent radius. This association, though further strengthened by the formation of a bridge or an arch, is to be regarded as only of secondary importance. The orientation of the ossicles of the lantern in the adult may, therefore, be as follows: compasses, rotulæ, and epiphyses radial; jaws and teeth interradial.

5. *The Rotulæ.*

Each of the five rotulæ is laid down in a radius of the "echinus-rudiment" in the metamorphosing larva, as a tri-radiate spicule, always with two rays directed towards the œsophagus and one ray turned in the opposite direction (Plate 11, figs. 1 and 2, *R.R.*). By the usual process, a broad, fenestrated, and more or less rectangular plate is formed, roofing over the two epiphyses below, which are thus concealed from an aboral view of the lantern at this stage (Plate 14, fig. 5). In this plate, the boundaries of the primordial tri-radiate spicule may still be traced. This stage recalls to one's mind the broad rotulæ found in *Palæodiscus ferox* (6).

6. *The Compasses.*

In the absence of any evidence to the contrary, the "compasses" have been usually regarded as unpaired elements. The bifurcated ends, however, were supposed by Sollas (5) to indicate their paired nature. But their development shows conclusively that, whilst they are duplex structures, the forked ends are not indications of a paired nature.

Each compass can be traced to a pair of tri-radiate spicules placed, not side by side, but in a radial line one behind the other (Plate 13, fig. 13, *I.C.* and *O.C.*). One may, therefore, speak of an outer spicule and an inner spicule with reference to the central axis of the lantern. Nor are these two spicules deposited at the same time as are those of the epiphyses, for instance; the inner first and the outer next is the rule. Further, these two spicules, though in the same line, occupy different positions and levels in relation to the rotula. The outer spicule is situated almost behind the rotula and almost at the same level as the latter, if not below it, whereas the inner spicule is placed just above the rotula. This fact accounts for the bent condition of the compasses in the adult.

These spicules differ somewhat in the manner of their growth, not only from the other members of the lantern, but also between themselves. One of the three rays of the inner spicule is absorbed gradually (Plate 12, fig. 3, *I.C.*) and the remaining two rays stretch end to end, forming a straight rod, more or less, directed radially. The free-branching and anastomosing of the original rays of the rudiment, found in the development of the rotula for example, does not obtain here. The next step in their growth consists in an increase in thickness by the appearance and coalescence of branches at the two ends of the rod; the middle part of the rod appears to grow in thickness all the same, though one does not see as many offshoots there.

The outer spicule has all the three original rays well developed; nevertheless they do not branch. Its growth is confined to its size. The three ends of the spicule appear in a late stage thick and fenestrated, but the body of the spicule is devoid of meshes (Plate 15, fig. 6, *COM.*). The tri-radiate shape is maintained intact and the ray directed centralwards meets the inner piece and forms a suture with it, thus constituting the adult compass. It is at this suture that the elevator muscles of the compasses are attached, some of the fibres to the hinder end of the inner piece and others to the proximal end of the outer. This suture between the two pieces is so complete in the adult echinoids, both extinct and living, that its double nature has been scarcely ever surmised except in one species *Strongylocentrotus dröbachiensis* (Jackson, R. T., p. 179).

The compasses are the only set of ossicles of the lantern which are absent in the "echinus-rudiment" of the larva, but appear after the metamorphosis.

7. *The Teeth.*

At the very outset it may be stated that the tooth is, in the lantern organisation, an element with a unique structure and a peculiar development.

Four stages may be recognised in its construction:—

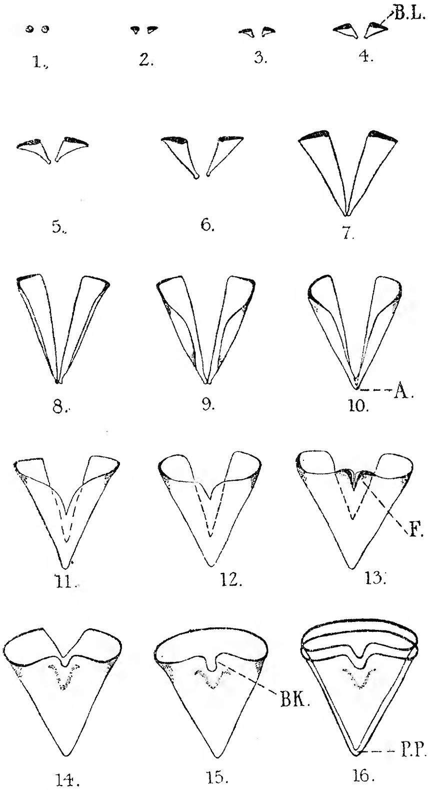
(1) The formation of a pair of primordial lamellæ;
(2) The deposition of secondary pairs of lamellæ;
(3) The consolidation of all these; and
(4) The attainment of a relatively stable position by the permanently active tooth-germs which will henceforth constitute the root-end.*

The earliest traces of a tooth, so far as I have made out, are an incipient cone, incipient in the sense that, not being completely closed on the outer side, it is a cone in making. It will be seen presently that each cone which comes into being subsequently arises from a pair of lamellæ. One may, therefore, reasonably infer that each of these five cones also arises in the same way from a pair of lamellæ. We shall accordingly call these five cones, the "first cones," and the pair of lamellæ of which each first cone is believed to be composed, the "pair of primordial lamellæ." Each first cone is situated in an inter-radius (Plate 11, fig. 1, *F.C.*), with its apex turned towards the future oral aspect and its base directed towards the future aboral aspect. This cone serves as a starting-point for the upbuilding of the entire tooth; for within the cavity of this cone in the metamorphosing pluteus are found deposited about six pairs of secondary lamellæ. The first cone remains as a distinct structure, even after a good bit of the embryonic tooth has come into being (text-fig. 3, *F.C.*); it is highly probable that finally it enters into union with its successor and forms the tip of the embryonic tooth.

A study of the numerous pairs of lamellæ deposited in succession after the first cone has been formed reveals several facts of no small importance and interest. Each lamella is laid down as a round calcareous particle, which, as I have evidence to show, is probably the product of a single calciferous cell. This particle grows by accretion of lime on one side only in such a way that a small triangular plate is first formed (Plate 11, fig. 1, *L*, and text-fig. 1). At the base of this plate a peripheral growth takes place in one plane, resulting in an imperforate transparent lamella. When it has attained its maximum vertical growth it has got the contour of an isosceles triangle, with its apex directed towards the ventral aspect and its base towards the aboral surface. Even before a particular lamella reaches its full size, fresh lamellæ are deposited at higher levels, one above the other, in quick and regular succession, always on the inner side of the preceding lamella. One can, therefore, read the several stages passed through by a single lamella from the series of lamellæ representing different stages in their growth (text-fig. 2).

---

* This fact will be elucidated in a paper on the soft parts of the lantern, now in preparation.



Text-Fig. 1.—Diagrammatic representation of the formation of a cone from a pair of calcareous particles. 1. A pair of calcareous particles. 2, 3, 4, 5, 6, and 7. Progressive stages in the formation of a pair of lamellæ; *B.L.*, Basal end of a lamella where growth takes place by accretion. 8. The pair of lamellæ has attained its maximum vertical growth, further increase taking place only at the lateral edges; the two lamellæ are undergoing slight bending due probably to the pressure of lamellæ subsequently deposited. 9 and 10. The inner lateral edges of the two lamellæ have commenced to grow; *A.*, The first spot where the latter come into contact and fuse. 11 and 12. The inner lateral edges have approximated and are gradually fusing; the outer lateral edges have also begun to join; it will be noticed that both the commencement and the completion of the fusion of these latter edges are later than those of the inner; this stage in the formation of a cone may be called the "incipient cone" stage. 13. The flange *F.*, at the top corner of each inner lateral edge, has appeared. 14. The same flanges have joined, forming the characteristic beak. 15. A complete cone; *BK.*, Beak. 16. Two cones showing their relation to each other; *P.P.*, the spot where the fusion between the apices of the two cones takes place, this being the foundation for the formation of an axial rod—the "pars petrosa."

The relative position of the two fellow lamellæ of a pair deserves notice. They are deposited in close proximity to each other, but do not touch, and also at different levels so that they alternate. As growth proceeds, however, the two fellow lamellæ are found at the same level, inclined, at first, towards each other at an angle which varies with their growth till, finally, as the result probably of pressure from succeeding lamellæ, their apices are brought into contact and fuse together.

At this stage of our investigation it is, perhaps, well to take into account certain fundamental facts revealed to us:—

(1) We see that a lamella does not pass through a tri-radiate spicule condition, unlike, in this respect, the other echinoderm ossicles which do, as far as is known at present.

(2) The growth of a lamella is unusual, being different from the normal method of ossicle-formation which obtains among the other component elements of the lantern.

(3) There is a maximum limit to the vertical growth of a lamella, further growth being along the two equal edges of each lamella.

(4) From the fact that numerous pairs of lamellæ go to build the adult tooth, two conclusions can be drawn, viz., (*a*) that the urchin-tooth is a paired structure, and (*b*) that a pair of lamellæ is the unit of the same. This admission of the morphological value of a pair of lamellæ as a unit is not, as will be seen later, prejudicial to regarding a cone formed by a pair of lamellæ as an integral structure.

The process of formation of the tooth from these paired lamellæ is not by any means simple.* When two lamellæ of a pair have attained their maximum vertical growth, by the pressure probably of the succeeding lamellæ above, they become bent and concave to an equal extent on their inner surfaces, their outer surfaces becoming correspondingly convex. During this bending the two lamellæ appear to grow along their lateral edges till those of one lamella face each to each their two fellows on the other lamella (text-fig. 1). This growth is maintained till the confronting edges meet and fuse, forming a characteristic cone.†

While the fusion of the inner edges is taking place, the rudiments of the carina are found to arise. An inwardly directed flange appears at the top corner of each inner edge (text-fig. 1). At about this time each cone undergoes a flattening from the inner to the outer side. Partly as the result of this flattening and partly owing to their growth, the above-mentioned flanges project well towards the œsophageal side. They ultimately come into contact

---

[*] Lovén's (3, p. 9) description of the formation of a tooth, in *Goniocidaris*, from a single row of lamellæ is extraordinarily simple. He says as follows: "The lamels, the general form of which corresponds with that of the tooth, are laid one upon another regularly from the top downwards." Spencer (1904, p. 36), likewise, figures a simple arrangement of lamellæ in *Palæodiscus ferox*.

[†] Théel (7) describes also a cone-in-cone arrangement in *Echinocyamus pusillus*.

and fuse forming a beak-shaped process somewhat like the beak of an ounce-glass. It will be seen that in the formation of this beak both lamellæ take an equal share. When several cones fit into one another, their beaks likewise fit together, thus giving rise to a crest which is the precursor of the carina of the adult tooth. The lower part of the tooth in the imago appears to be devoid of this crest; only the cones arising later develop the beaks in question.

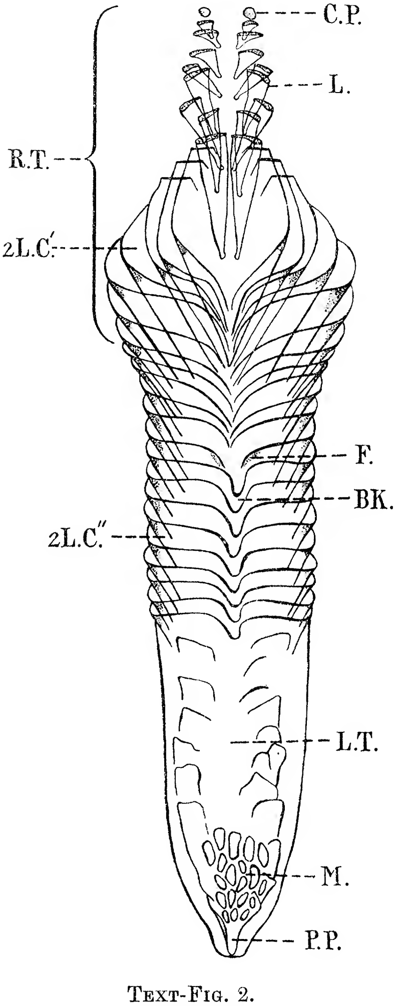
The fitting into one another of the cones takes place in such a manner that the brim of an upper cone always projects a small distance from above the brim of the lower cone into which it is enclosed. This fact has a necessary bearing, first, on the growth of a carina on the inner side and, second, on the formation probably of the middle furrow on the outer side of each tooth (Plate 15, fig. 6, *CA.* and text-fig. 1).

In the aboral end of the embryonic tooth—the root-end in the adult—one can see all the intermediate stages between a pair of calcareous particles, the simplest condition of a pair of lamellæ, and a transparent beaked cone, the most advanced stage of the same (text-fig. 2). As has been already mentioned, the first point of contact and fusion between every two lamellæ of a pair is at their apices. The fused apices of one pair unites with those of its predecessor and successor even before the pair itself reaches the stage of a cone. Thus a central rod results to which are attached all the cones and the younger pairs of lamellæ. Presumably this rod is the "pars petrosa" of Giesbrecht (1, p. 90). Curiously enough, the first cone does not appear to participate in the formation of this stony part (text-fig. 3).

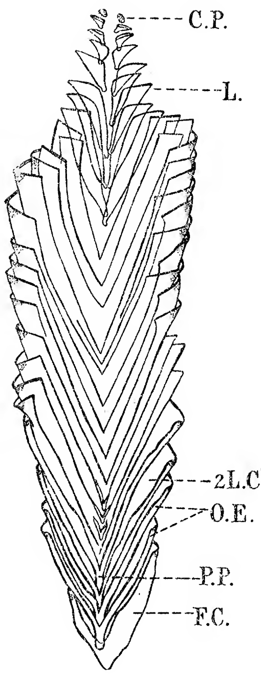
It has not been possible to follow closely the next phase in the building of the tooth. The coalescence of the cones appears to proceed centripetally from the "pars petrosa" outwards. The outlines of the cones gradually disappear owing to the fusion of their walls.

The median furrow of the adult tooth probably marks the place where the suture of the two outer edges of a pair of lamellæ is formed. Of this line of junction a greater portion is bound to disappear in the process of coalescence owing to its internal position in the cavity of its predecessor as explained already; only the small exposed parts of this suture in the several cones probably persist and contribute to the formation of the median furrow.

On account of the relative position between every two cones, the beaks are, on the inner side, the only exposed parts of the line of junction between the two inner edges of the pairs of lamellæ. It must be observed that no indication of a suture, however, is to be found on each beak. These beaks, as has been already described, are the precursors of the carina which is for this reason a composite paired structure. Such is the construction of a tooth so far as one could make out from observations of hard structures.



TEXT-FIG. 2.



TEXT-FIG. 3.

TEXT-FIG. 2.—Reconstruction of a fairly advanced tooth as viewed from the inner side. *R.T.*, Root-end of the tooth where the lamellæ can be seen in all their progressive stages; *C.P.*, Calcareous particle, the first beginning of a lamella; *F.*, Flange; *L.*, Lamellæ: 2 *L.C.′*, Two lamellæ in the process of cone-formation; 2 *L.C.″*, A fully formed cone; *BK.*, The beak of a cone; *L.T.*, Lower part of the tooth where the walls of the cones have fused; *M.*, Mesh-work formed by the coalescence of lamellæ; *P.P.*, "Pars petrosa," or the stony part.

TEXT-FIG. 3.—Actual drawing of a tooth less advanced than the one shown in text-fig. 2, viewed from the outer side; the first cone is still intact; it will be noticed that the cones are yet imperfect on the outer side, fusion between the edges thereof being considerably delayed; *F.C.*, First cone; *P.P.*, the "Pars petrosa," or the stony part resulting from the union of the apices of the serially fitting cones; 2*L.C.′*, Two lamellæ in the process of cone-formation; *L.*, Lamellæ; *C.P.*, Calcareous particle; *O.E.*, Outer edges not yet approximated.

8. *Discussion.*

In the mouth-frame of recent Asteroidea as well as in most of the fossil star-fishes are seen five pairs of generally triangular ossicles situated in the inter-radial angles bordering the mouth (Spencer, 1913, p. 26). Originally identified by Ludwig as the first pair of modified adambulacrals, they are now known as mouth-angle plates. By their position both in the embryo and in the adult and by their relation to the mouth, the five pairs of "alveoli" of the lantern of Aristotle recall the five pairs of mouth-angle plates in star-fishes.

In the section on "epiphyses," we saw how the two epiphyses each situated on an alveolus belonging to adjacent jaws constituted a pair, and not the two epiphyses which formed an arch. As the radial canal of the water-vascular system runs between the two epiphyses in question,* there is no serious obstacle to regarding this pair as corresponding to a pair of ambulacral ossicles.

The interpretation of the rotulæ offers undoubtedly great difficulties. These are not only odd elements as conclusively shown by their origin but also the sole unpaired elements in the lantern of Aristotle. The only odd ossicle which gets into touch with the mouth-frame in extinct star-fishes is the odontophor. In an account of the family Urasterellidæ, Spencer (1913, p. 135) observes as follows :—"In a private letter to me . . . . Hudson asks me to note (in the mouth-frame of the American species *Urasterella pulchella*)† 'paired muscle remains . . . . just within the large inter-radial (odontophor).' He goes on to state that there must have been muscles to draw in the mouth-angle plates, which in each inter-radius acted as an outer jaw. The origin of these adductors may have been on the inner surface of the odontophors rather than on the first ambulacralia." This indicates that in certain asteroids the odontophor may get into close relationship with the mouth-angle plates. It must be noted, however, that in the lantern of Aristotle the rotula has muscular connection with the epiphyses and not with the jaws.

In certain other fossil star-fishes again, the odontophor has been shown to occupy an internal position (Spencer, 1917, p. 180). I quote these two features of the odontophor in the extinct asteroidea in order to show how this odd ossicle behaves in certain cases, it being far from my purpose to suggest thereby any asteroid descent for the echinoids.

The great impediment to regarding the rotulæ as modified odontophors is the fact that, while the latter are inter-radial, the former are radial. Can it be that, after occupying an internal position in the ancestral urchin, the odontophors underwent a sinistral or dextral rotation which brought them to a radial position? MacBride* with reference to the inter-pyramidal muscles says as follows: "These on contraction, approximate the pair of jaws into which they are inserted, and it will easily be seen that by the successive contraction of the five comminator muscles a rotating movement of the teeth would be produced which would cause them to exert an action something like that of an auger." Can this action of the lantern, coupled with the fact that the rotulæ alone of all the ossicles of the lantern are free from muscular attachment with the shell, be supposed to have brought about this displacement?

---

* This fact will be elucidated in a paper now in preparation.

† This parenthesis is mine.

From its double origin and radial position each compass may be regarded as corresponding to a pair of ambulacral ossicles. It is generally known that in certain extinct star-fishes, the paired ambulacral plates alternated with each other. If the same condition had prevailed among the ancestors of urchins, one might conceive of a displacement consisting of one member of a pair being pushed in front of his fellow.

In instituting a comparison between a tooth and other ossicles of the lantern or those of the mouth-frame of star-fishes, one should take a pair of primordial lamellæ to represent a tooth on the one hand and paired ossicles on the other. For I hold an urchin-tooth is not, in the strict sense of the term, an ossicle; it is an aggregate of paired ossicles if the lamellæ can be so called. Whether the lamellæ themselves are ossicles is open to doubt; as we saw in their development, they neither pass through a tri-radiate spicule stage nor do they grow into fenestrated plates as ossicles of echinoderms do in general by the branching and anastomosing of calcareous offshoots. On the contrary a tooth-lamella grows by accretion confined in the early stages to one particular side, viz., the base of the minute triangular plate. For purposes of comparison, therefore, a pair of tooth-lamellæ may be, with the above-mentioned reservations, taken to represent a pair of ossicles corresponding to a pair of "alveoli" or "epiphyses" rudiments. This being so, a whole tooth does not stand in the same relation to its rudiments as the other component parts of the lantern do; the latter are, *par excellence*, echinoderm ossicles whereas the former is an aggregate of paired structures which are not undoubted ossicles. An epiphysis for instance, being the direct outcome of a tri-radiate spicule, is a unit in itself; but a tooth is an aggregate, being the product of several paired units, the lamellæ. A tooth is essentially a double structure like a pair of "alveoli" or "epiphyses," the only indication of this in the adult tooth being the median furrow which runs longitudinally along its outer side.

The homologues of the urchin-tooth are to be looked for among the bristles carried by the mouth-angle plates in star-fishes. If two such bristles get flattened, assume a cone-shape, and are pushed between the two mouth-angle plates thus becoming partly internal, we have the rudiment of an urchin-tooth.

---

* See "Echinodermata," 'Cam. Nat. Hist.,' p. 526.

There must have been several physiological forces at work in the evolution of the urchin-tooth. First of all, the liability to wear and tear of an organ used for browsing purposes could have induced the permanent retention of the activity of the embryonic tooth-germ. The ancestor of the sea-urchin, whoever that might have been, let us suppose, started with the five first cones; these may well have served the primitive animal as organs of mastication. If the ancestral animal browsed on things like the brown fronds of *Laminaria* or bored into rocks*—certain sea-urchins are known to do both—the conical teeth would be liable to suffer decay. Under such circumstances, the power of replacing worn-out teeth would have been of immense advantage, and hence the permanent activity in the adult of the five embryonic tooth-germs was probably the primary factor in the evolution of the urchin-tooth.

But how can one account for the coming into being of a stout rod as the result of fusion of several pairs of lamellæ? What could have induced the deposition of numerous pairs of lamellæ, one above the other, in the imago urchin, while even as yet the mouth is not formed? Efficiency is the first answer that suggests itself. A short conical tooth, formed by a pair of delicate lamellæ and renewed frequently, even at its best must have been but a weak instrument to the ancestral urchin. If the tooth-germs laid down precociously pairs of lamellæ, and if by the fusion of these a stout rod resulted, that meant efficiency in function and advance in structure. In this way, one may account for the formation of a stout rod-shaped tooth through the fusion of several cones.

In this connection, perhaps, it will be well to consider what reaction the evolution of the tooth may have had on the jaws. Each tooth in the adult is closely and immovably attached to a jaw. This being so, the jaw is bound to respond to any adaptations of the tooth. In the "echinus-rudiment," the vertical height of the lantern is at its minimum.† Now, if the tooth increases in length in accordance with the causes indicated, it is extremely likely that there will be a corresponding response on the part of the jaw to adjust itself to the growing tooth. That the tooth may well have been the leading factor in the evolution of a high lantern is perhaps seen in the lantern of the metamorphosing pluteus (Plate 11, fig. 1, *L*). Here we find that, even while the two jaw-rudiments are in the tri-radiate spicule stage, the tooth is in a relatively higher state of development with the first cone and nine pairs of secondary lamellæ; and it extends aborally beyond the limits of the jaw-rudiments. It is perhaps admissible to infer from this that, with the growing length of the tooth, the jaw-rudiments kept pace *pari passu*, and the result was a lantern of great height.

---

* *Vide* "The Locomotor Function of the Lantern in Echinus," by Prof. Gemmill, 'Roy. Soc. Proc.,' vol. 85, p. 101 (1912).

† The height of the lantern in *Palæodiscus ferox* is small when compared with that of living urchins (Spencer, 1904).

"Summarising the foregoing conclusions, I regard the lantern of Aristotle as homoplastic with the buccal armature of star-fishes; the pyramids are the modified first adambulacral plates; the epiphyses have arisen from the first ambulacral plates of the Echinoid series; and the teeth represent the odontophore, which has acquired a persistent root; the radius and rotula remain problematical." So wrote Prof. Sollas in the year 1899 in his paper on "Silurian Echinoidea and Ophiuroidea" (5). I leave the reader to compare this statement with what has been indicated on the homologies of the lantern of Aristotle in this paper. It will be seen that the idea of the homology of the urchin-tooth advanced by me is entirely new, and based on indisputable embryological facts.

9. *A Comparison between Giesbrecht's* (1)* *Account of the Development of the Urchin-tooth as revealed by its Root-end in the Adult and the Construction of the Same as seen in the Young Urchin.*

Attempts to probe into the peculiar construction of an urchin-tooth were made even as early as the year 1841. Beginning with Valentin,† Meyer, Waldeyer, Leuckart, Giesbrecht, Lovén, Théel and MacBride successively each gave his attention to this organ. With the exception of Lovén, Théel and MacBride, who studied it in young urchins, these authors employed in their researches the root-end of the adult urchin-tooth. The credit of our knowledge that the urchin-tooth is built up of lamellæ is largely due to these workers. Nevertheless, our ideas as to the manner of the origin of these lamellæ, their growth, arrangement and significance have hitherto been rather imperfect. The first attempt, I may say, to interpret the tooth-structure in terms of biogenetic laws has been made in this paper (see Discussion).

A very interesting study was made by comparing my own observations, based on the embryonic tooth, with those obtained by the examination of the root-end of an adult tooth. From the nature of the case one should expect the process in the adult to be similar to that in the young. Hence a comparison between the two is inevitable, nay, compulsory. I am bound to confess that my own researches do not confirm in their entirety the conclusions drawn by Giesbrecht, the last and most important of the investigators of the root-end of the adult urchin-tooth.

---

* The greater part of this important paper was translated to me by Prof. MacBride.

† "Anatomie du genre Echinus," 1841, by G. Valentin, the first monograph in 'Monogr. d'Echinodermes viv. et foss.,' published by L. Agassiz.

According to his observations there are two sets of units for the urchin-tooth, one for the wings or the lateral parts and the other for the carina. The units of the former are flat structures called "Scales" (Schuppen), which are not homogeneous but are made of two lamellæ separated by a narrow interspace. It appears to me that, in this latter inference, Giesbrecht has been misled by an artifact, and, likewise also in his other, mentioned in the context, that his second set of units, "the prisms," have an axis-cylinder. Each scale is undoubtedly a homogeneous structure of integral value. For this reason, and also because it is more appropriate, I have, in the description of these plates, retained the use of the term "lamella," and dropped out the word "scale." His account of the manner of growth of each "scale" is not in perfect accord with mine. He says: "Meanwhile, quite like the shell of a mussel, lime is deposited in layers round one 'initial point' (the 'calcareous particle' in my description),* though not uniformly in a circle but on one side only, so that the initial point always remains at one edge of the plate like the umbo of a mussel shell." Though this description suggests a peripheral growth, it differs in two respects: (1) the growth in the pre-cone-formation period is by accretion in a straight line along the base of the triangular plate (text-fig. 1); and (2) the concentric rows of stripes he mentions in the context are non-existent in the lamella. Further, Giesbrecht describes the lamellæ of one row as alternating with those of the other, and has entirely missed out the formation of the cones.

To me, it would appear, that his second set of units—what he calls "prisms," but, in reality, long needle-shaped structures—is of the nature of secondary calcification. In the young imago, the carina is found to arise solely by the fusion of inwardly directed flanges (text-fig. 1) of the incipient cones, as has been already described in the section on teeth. Giesbrecht himself speaks of a certain part of the lamella taking part in the formation of the carina. I cannot, therefore, agree to his giving the "prisms" a morphological value equal to that of the lamellæ.

On account of the nature of the methods he employed, such as dissecting the root-end with a mounted-needle and making ground-sections (Dünnschliffen) of the same, I do not know how far one can rely on these doubtful details of his observations. He boiled the root-end with caustic-potash, a treatment which undoubtedly would have interfered with the structure of such delicate things as the lamellæ. The wonder is that Giesbrecht accomplished so much with the methods at his disposal in those days.

---

* The parenthesis is mine.

10. *Summary.*

(1) All the calcareous elements of the lantern of Aristotle, with the exception of the teeth, are deposited as tri-radiate spicules; in this, as well as in their further growth, they resemble the ossicles of echinoderms in general.

(2) The two "epiphyses," one on each side of and below a rotula, are to be regarded as constituting a pair.

(3) A "compass" arises from two rudimentary spicules. It is the only element of the lantern absent in the "echinus-rudiment."

(4) A tooth is a paired structure in consequence of its composition of a double row of lamellæ. A pair of lamellæ is its ultimate unit, although it is not inconceivable that originally a pair of lamellæ itself, after assuming a cone-shape, could have functioned as an integral structure, a primitive kind of tooth, in the ancestral urchin. There is a remarkable stage in the consolidation of these lamellæ, viz., the cone-in-cone arrangement. The carina is formed by the beaks of the serially-fitting cones.

(5) Without committing one's self to the view of a direct descent of the sea-urchins from the star-fishes, one may institute a brief comparison between the ossicles of the lantern and those of the mouth-frame of a star-fish: a pair of "alveoli" corresponds to a pair of mouth-angle plates; a pair of "epiphyses," as understood in this paper, to the first pair of ambulacrals; a pair of compasses to the second pair of ambulacrals; the rotula may, tentatively, be regarded as a displaced odontophor; the pair of primordial lamellæ, the forerunner of the urchin-tooth, may be compared to a pair of bristles attached to a pair of mouth-angle plates.

11. REFERENCES.

(1) Giesbrecht, W. (1880). "Der feinere Bau der Seeigelzähne," 'Morph. Jahrbuch,' vol. 6.

(2) Jackson, R. T. (1912). "Phylogeny of the Echini," 'Mem. Bos. Soc. Nat. Hist.,' vol. 7.

(3) Lovén, S. (1892). "Echinologica," 'Bihang Kongl. Sven. Veten. Akad. Handl.,' vol. 18.

(4) MacBride, E. W. (1903). "The Development of *Echinus esculentus*, together with some points on the development of *E. miliaris* and *E. acutus*," 'Phil. Trans. Roy. Soc.,' B, vol. 195.

(5) Sollas, W. J. (1899). "On Silurian Echinoidea and Ophiuroidea," 'Quart. Jour. Geol. Soc.,' vol. 45.

(6) Spencer, W. K. (1904). "On the Structure and Affinities of *Palæodiscus* and *Agelacrinus*," 'Roy. Soc. Proc.,' vol. 74. (1913 and 1917).—"A Monograph of the British Palæozoic Asterozoa," Palæontographical Society.

(7) Théel, H. (1892). "On the Development of *Echinocyamus pusillus*," 'Nova Acta Roy. Soc. Scien., Upsala,' vol. 15.

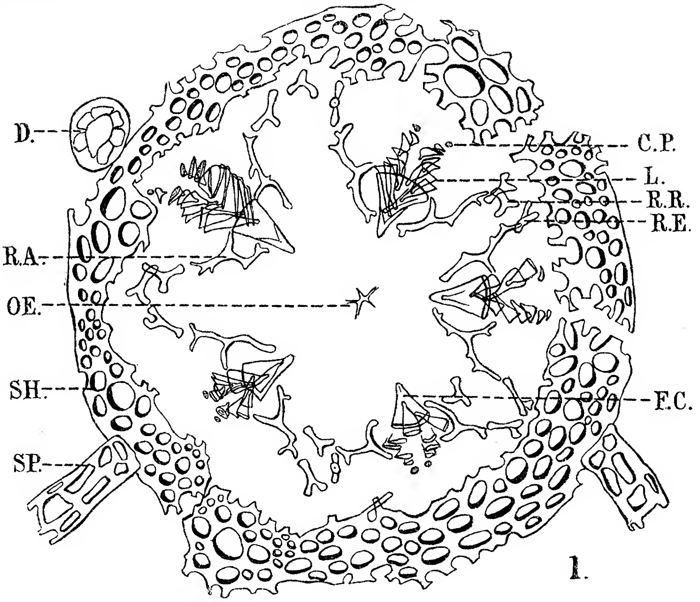
(8) Ubisch, L. V. (1913) "Die Entwicklung von *Strongylocentrotus lividus*," 'Zeit. Wissen. Zool.,' vol. 106, Part III.

EXPLANATION OF PLATES.

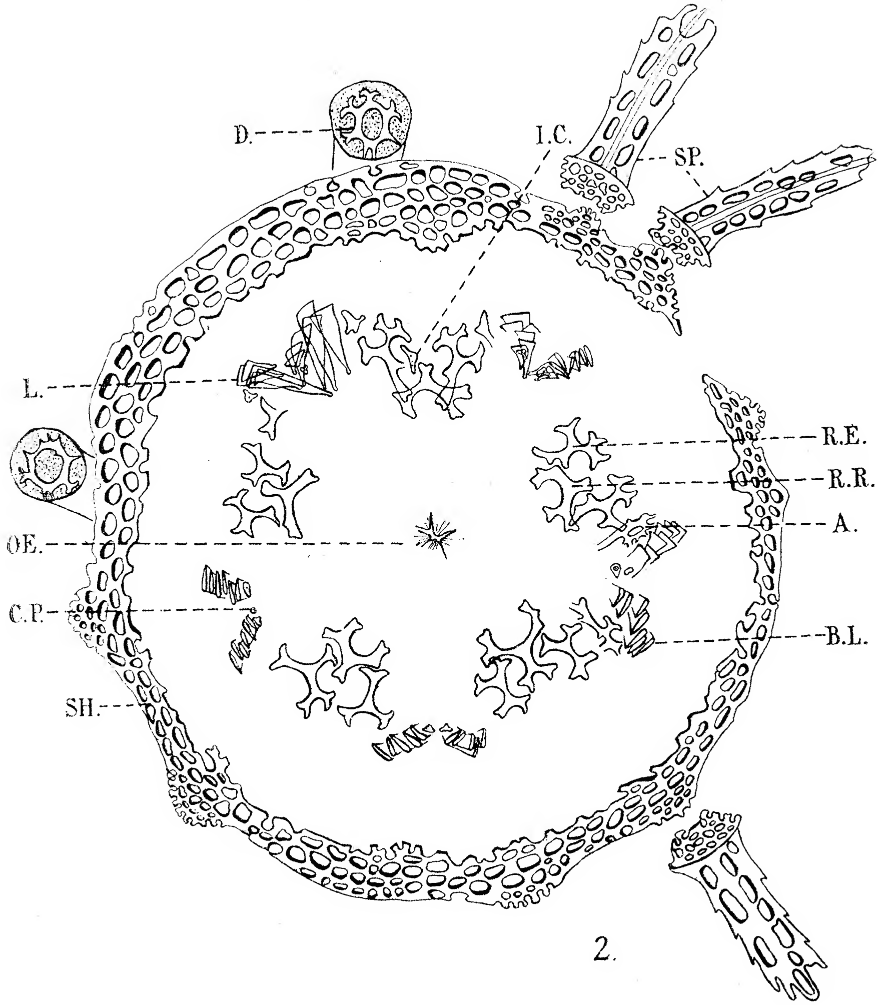
LIST OF ABBREVIATIONS USED.

A.	Alveolus.
B.	Boss of a spine.
BK.	Beak of a cone.
B.L.	Basal ends of lamellæ.
CA.	Carina of a tooth.
C.P.	Calcareous particle—the starting point of a lamella.
COM.	Compass.
D.	Calcareous disc of a tube-foot sucker.
E.	Epiphysis.
EL.M.	Elevator muscles of a compass.
F.	Flange of a lamella.
F.C.	First cone.
I.C.	Inner rudiment of a compass.
IN.M.	Inter-pyramidal muscles.
L.	Lamellæ of a tooth.
2*L.C.*′	A pair of lamellæ in the process of cone-formation.
2 *L.C.*″	A fully formed cone.
O.C.	Outer rudiment of a compass.
OE.	Œsophagus.
O.E.	Offshoot of an epiphysis.
O.T.	Oral end of a tooth.
P.E.	A pair of epiphyses.
R.	Rotula.
R.A.	Rudiment of an alveolus.
R.E.	Rudiment of an epiphysis.
R.T.	Root-end of a tooth.
R.R.	Rudiment of a rotula.
SH.	Shell.
SP.	Spine.
S.C.	Suture between the two rudiments of a compass.
S.E.	Suture between the processes of two epiphyses.
T.	Tooth.

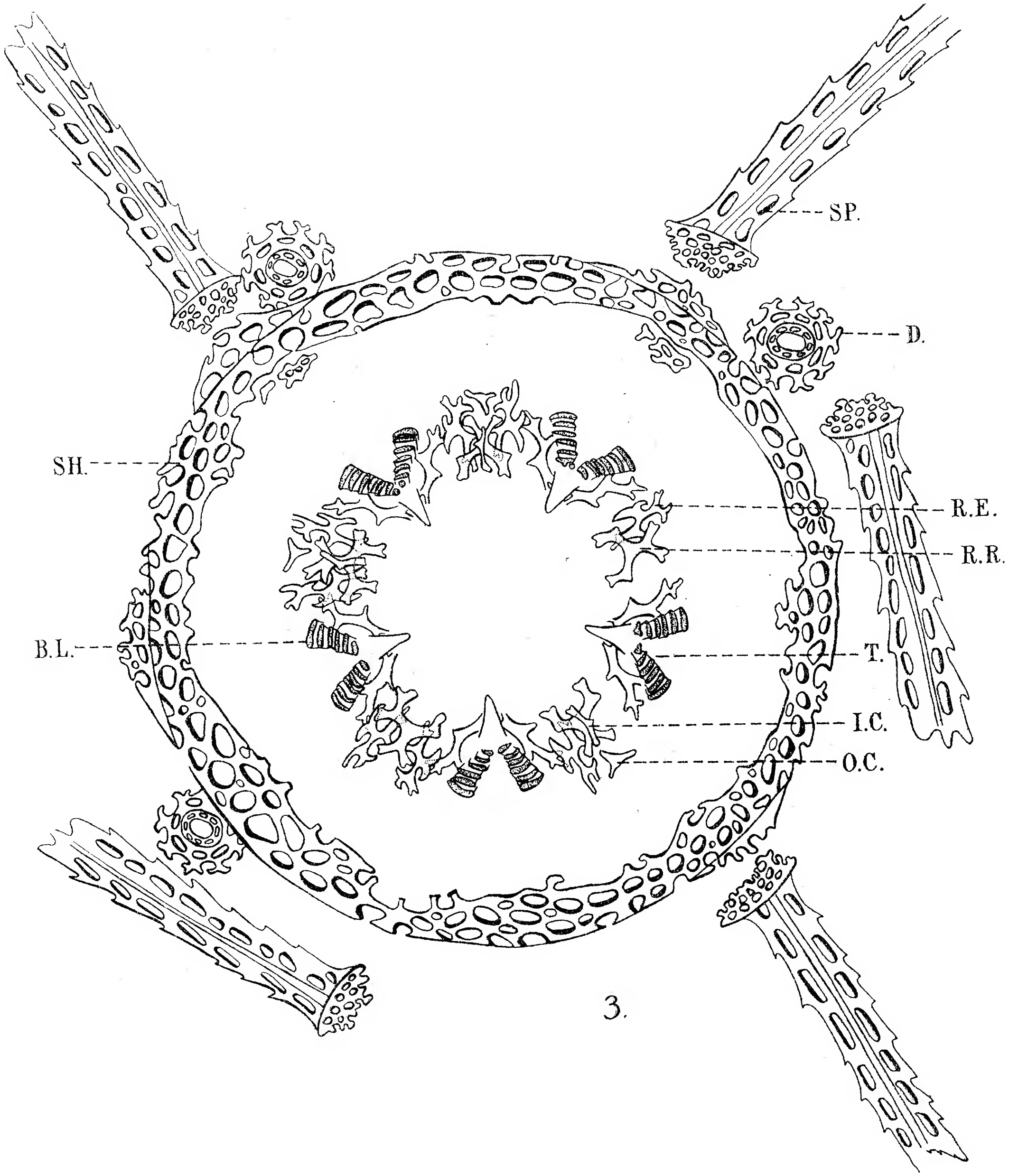
As the six figures form a progressive series, all of them should be consulted with regard to any particular ossicle of the lantern of Aristotle.



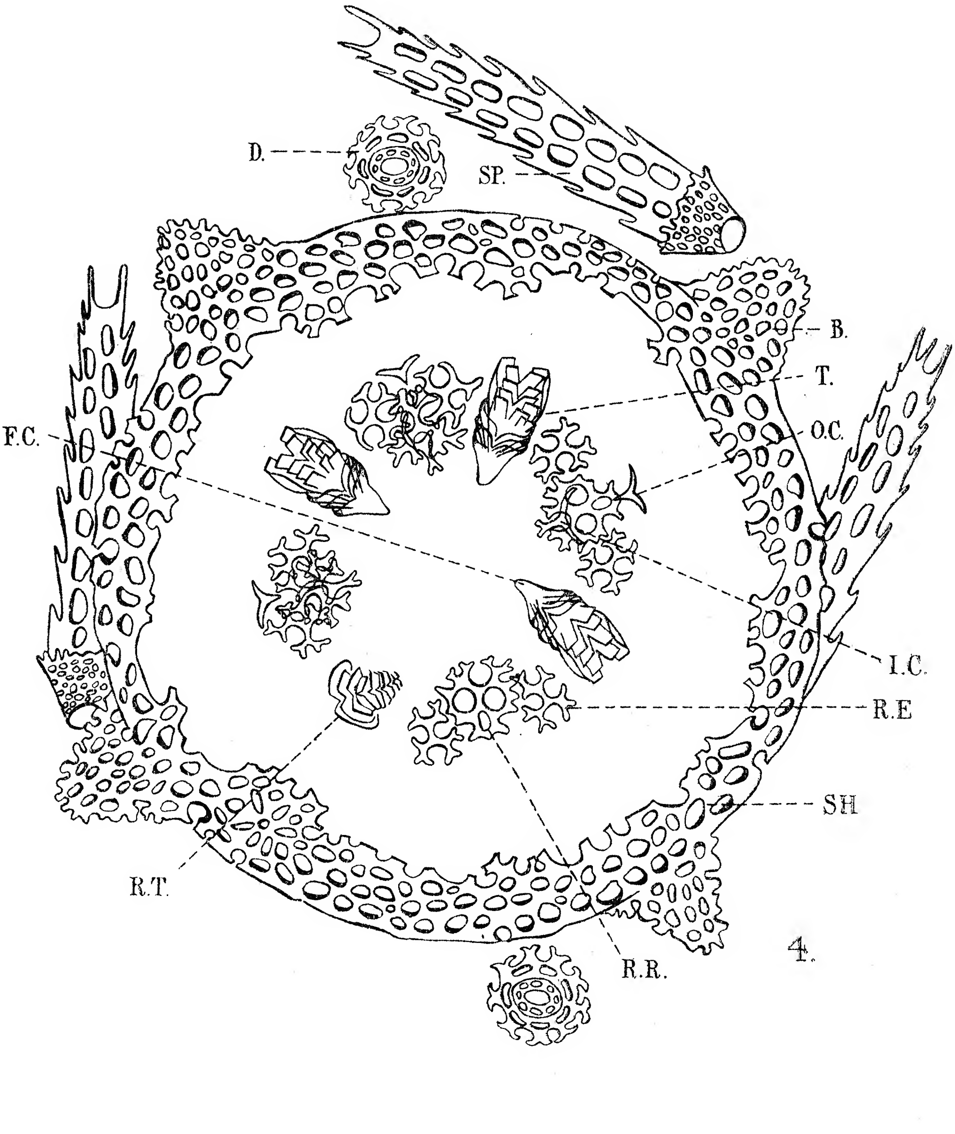
1.



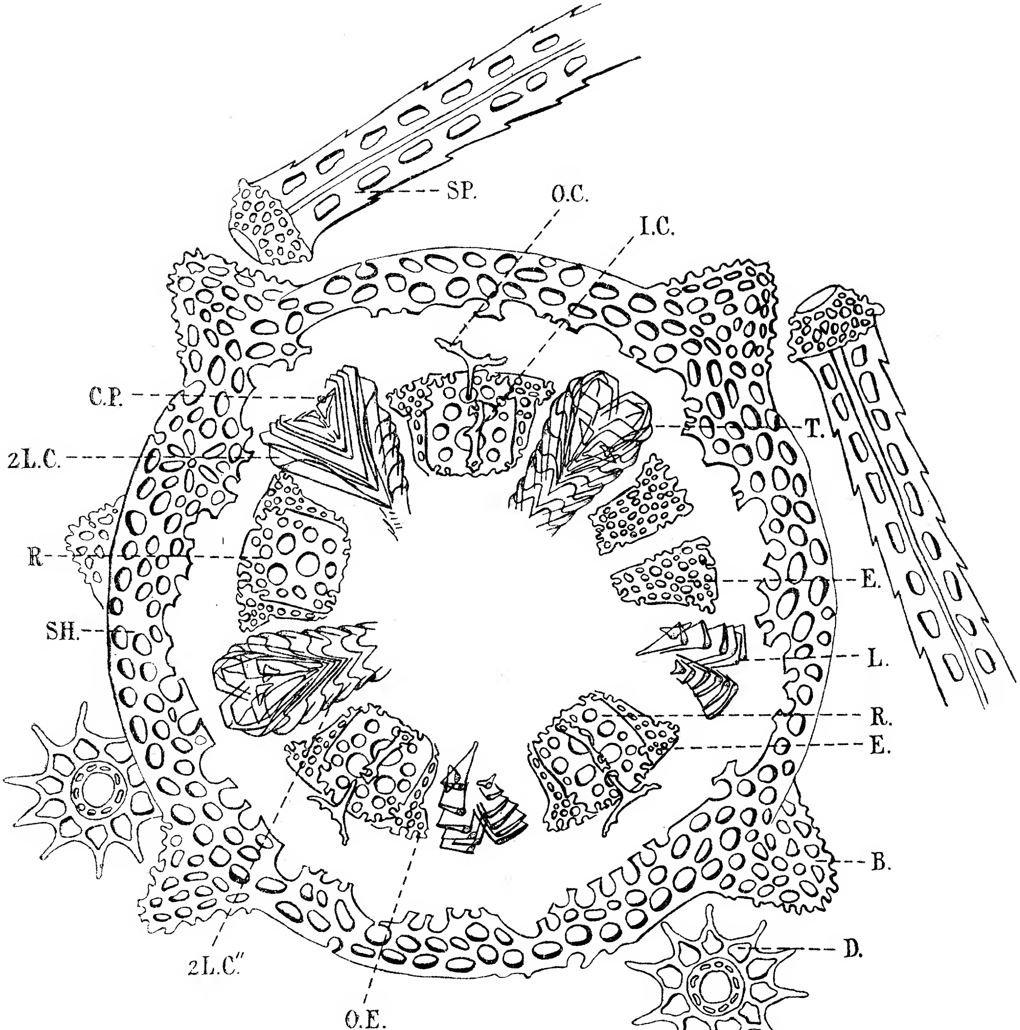
2.



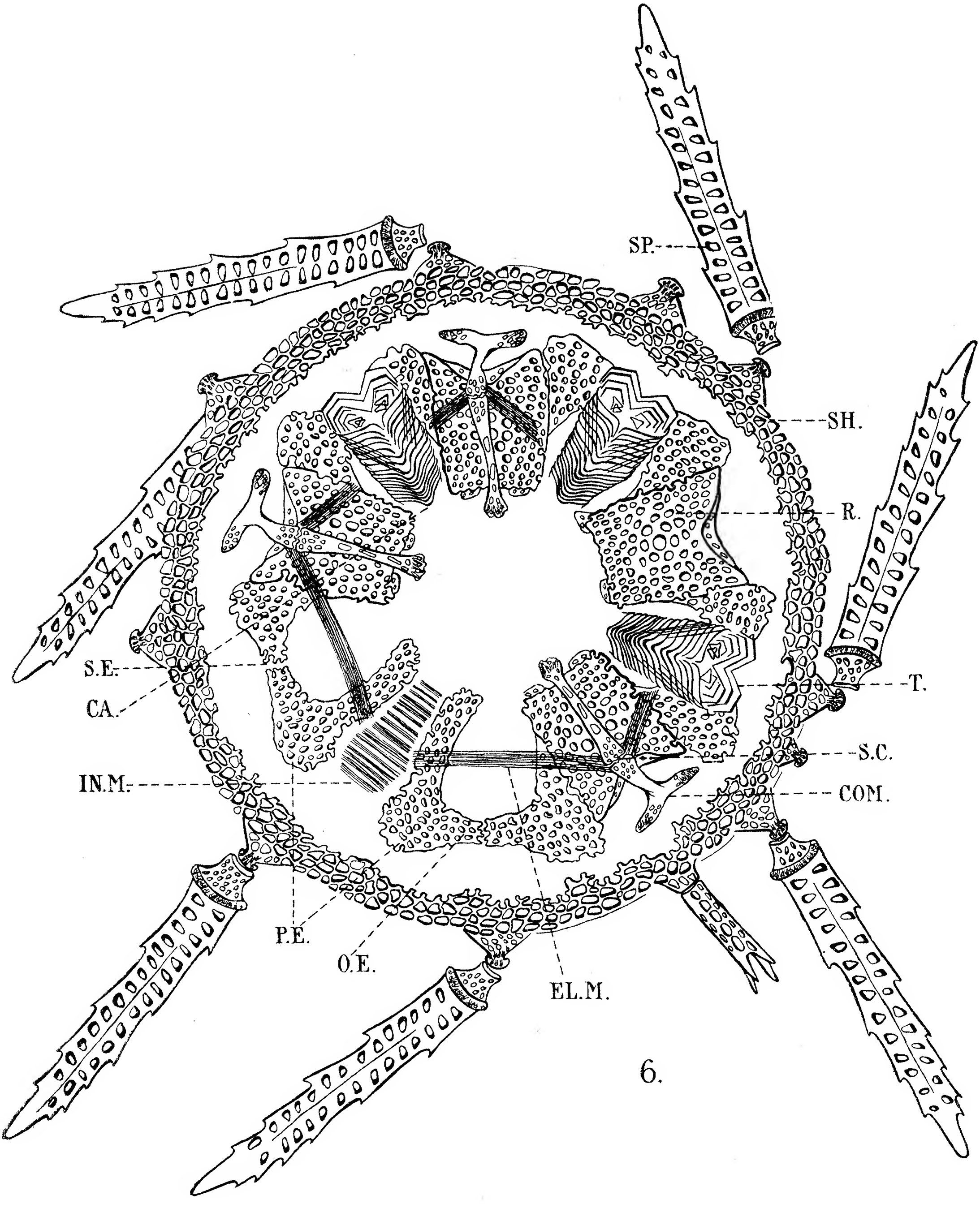
3.



4.



5.



6.

DESCRIPTION OF PLATES.

PLATE 11.

Fig. 1.—"Echinus rudiment" of a metamorphosing pluteus; macerated after all the extra-larval parts have been removed by sectioning; the lantern elements are seen from the future aboral surface; they are all, with the exception of the teeth, in the stage of tri-radiate spicules; no trace of compasses.

Fig. 2.—Aboral view of the lantern elements in a young imago, probably just metamorphosed; the top part of the shell has been removed and the specimen macerated; the inner rudiment of a compass visible in one radius; branching of the rays has commenced in all the spicules.

PLATE 12.

Fig. 3.—Aboral view of the same in an imago-urchin slightly more advanced; well-marked rudiments of the compasses are laid down in all the radii; epiphyses considerably branched; the teeth are rather diagrammatically represented.

PLATE 13

Fig. 4.—Aboral view of the same in imago still more advanced; the first branches of each rotular rudiment have joined end to end and fresh off-shoots have been put forth; one ray of the inner rudiment of each compass is in process of resorption and another ray is being lengthened to meet the outer rudiment; beaks are not formed by the earlier-produced cones; the root-end of a tooth shows the characteristic bend of the same seen in the adult; a compass has been omitted in one radius; it will be noticed the specimen is tetramerous in symmetry.

PLATE 14.

Fig. 5.—Aboral view of the same in imago more advanced than the one shown in fig. 4; the rotulæ and the epiphyses have grown into fenestrated plates; the outline of the original spicule may yet be traced in each rotula; the two rudiments of each compass are still separate; the epiphyses are putting forth processes; the alveoli are not visible; the compasses in two radii and a rotula in one radius have been omitted.

PLATE 15.

Fig. 6.—Aboral view of the same in a fairly grown young urchin; the rotulæ are beginning to sink between the two epiphyses below; the off-shoots of the latter have nearly met across the "foramen magnum"; the two pieces of each compass have met and formed a suture; a carina in each tooth can now be distinctly seen; the jaws are not visible; a rotula and a compass have together been omitted in one radius in order that a pair of epiphyses may be brought into view; likewise, the teeth have been left out in two radii to show the bridge formed by the processes of two epiphyses; the compass alone has been omitted in one radius to bring a rotula into full view.